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THE CIRCULATORY AND NERVOUS SYSTEMS OF
THE GIANT SCALLOP (*PECTEN TENUICOSTATUS*,
MIGHELS), WITH REMARKS ON THE POSSIBLE
ANCESTRY OF THE LAMELLIBRANCHIATA, AND
ON A METHOD FOR MAKING SERIES OF ANA-
TOMICAL DRAWINGS.

GILMAN A. DREW.

In considering any system of organs it is essential that we should bear in mind the modifications of the possessor of the organs, that adapt it to its particular life.

Pecten is one of the ablest swimmers among lamellibranchs. The whole structure of the animal is modified for this purpose. The valves have become rounded in outline, flattened, and comparatively light. The anterior adductor muscle has been lost, and the posterior adductor muscle, which is very powerful, is situated near the middle of the body. The cartilage has become well developed, so the shell may be opened quickly when the muscle relaxes, and the hinge line is straight, so there may be no unnecessary strains in opening and in closing the shell. Each gill is attached by one lamella only, so water in the temporary cloacal chamber may be thrown out without injuring the gills, and the gills and margins of the mantle are provided with muscles to withdraw them from the margins of the shell when the shell is closed. Furthermore the margins of the mantle are provided with infolded ridges and with circular muscles so it is possible to direct the current of water which issues from the shell in the required direction.

To fit the animal to a life of such activity, and to enable it to live in the comparatively exposed positions that it inhabits, an abundance of sense organs, tactile and probably visual, have been developed. These are placed in the most exposed positions, where they may give warning to their possessor, and are

¹ Free use has been made of both descriptions and figures published as No. 6 of the University of Maine Studies, under the title of "The Habits, Anatomy, and Embryology of the Giant Scallop (*Pecten tenuicostatus*, Mighels)."

accordingly borne along the margins of the lobes of the mantle.

It is not entirely certain what relationship *Pecten* bears to the usual form of lamellibranch as regards positions of parts. In lamellibranchs that are supplied with two practically equal adductor muscles, a line connecting the two adductors runs nearly lengthwise of the animal. In such a case the hinge line is more or less dorsal, one end is anterior, and the other posterior. When one of the muscles disappears, as is the case with *Pecten*, one of the landmarks disappears and it becomes more difficult to locate the direction of parts. Inasmuch as the hinge line is usually dorsal, it is very natural to look at the hinge line of this form as dorsal, and for matters of description it is convenient to so consider it. If, however, the position that the anterior adductor would have occupied, had it been retained, be considered, the position of the mouth, foot and heart indicate that it would have to be placed much nearer the hinge line than the present position of the posterior adductor muscle, the muscle that is retained. If this is the case, it becomes evident that the loss of the anterior adductor muscle has been accompanied by a general reduction of the anterior part of the body, so a large part of the body of *Pecten* is to be considered morphologically posterior. This supposition seems to be borne out by the nervous system, and the vascular system of the mantle, as well as by the extent and position of organs. In most forms the margin of each lobe of the mantle is supplied with a posterior and an anterior pallial nerve of approximately equal size. These nerves supply the muscles and sense organs of the margins, and, in many forms at least, unite with each other so they form a continuous connective between the cerebral and the visceral ganglia. In *Pecten*, not only is this the case, but the nerve in the margin of the mantle is joined at intervals for nearly its whole length by nerves from the visceral ganglion (Fig. 6). On the other hand, it is joined only in the region of the anterior ear by nerves from the cerebral ganglion. The visceral ganglia are the important ganglia of the animal, and both the cerebral and pedal ganglia are greatly reduced.

The blood is supplied to the mantle very largely by the posterior pallial arteries (Fig. 5). The anterior pallial arteries are

comparatively small, and while they are connected with the posterior pallial arteries, the size and character of the vessels indicates that the junction is probably very near the anterior ear.

Considering everything, it seems likely that the longitudinal axis of the body could be morphologically represented by a line drawn from near the hinge extremity of the anterior ear to the middle of the adductor muscle, and that a very small portion of the scallop is anterior.

CIRCULATORY SYSTEM.

The animal is large enough to allow one to successfully inject the chief vessels with starch or gelatin injecting mass, and then by dissection and microscopic preparations to trace the distribution of the vessels of the different organs and to determine quite definitely the course taken by the blood in its circulation.

The heart is a typical, symmetrical lamellibranch heart, with two auricles and one ventricle (Figs. 1 and 3), the latter perforated by the intestine which enters it near one end and leaves it near the other end (Fig. 2). Dorsally the ventricle is prolonged somewhat, posterior to the intestine, where the morphologically anterior aorta is given off, and ventrally to a less extent it is prolonged anterior to the intestine, where the much smaller morphologically posterior aorta is given off. The walls of the ventricle are of about even thickness throughout their extent, and are quite smooth outside and inside. The auricles join the ventricle on each side near its middle, are somewhat triangular in shape, with the most acute angle receiving blood from the gills and mantle at a point dorsal to the adductor muscle and directly ventral to, but some distance from, the cartilage. The opening of each auricle into the ventricle is near the middle of the side of the auricle that lies next to the ventricle and farthest away from the opening where the auricle receives its blood. The muscles around the openings of the auricles into the ventricle, and to a less extent around the openings through which the auricles receive blood, are well developed and must act as sphincters that tend to keep the blood from being regurgitated. The walls of the auricles, unlike those of the ventricles, are roughened by pits that open into the cavities of the auricles.

Both auricles and ventricle are composed of interlacing muscle fibers, and are capable of great extension. In preserved specimens, the heart is usually contracted and is not very conspicuous. In such contracted hearts the cavities of auricles and ventricle are practically obliterated.

The heart lies in a somewhat triangular, spacious pericardial cavity that is dorsal to the posterior half of the adductor muscle, and ventral to the posterior portion of the liver. Posteriorly it is covered only by a somewhat thick, muscular membrane which separates it from the mantle chamber.

As already mentioned, two blood vessels leave the ventricle (Figs. 1 and 3), one from each end. Although they are not so placed in reference to the ways the terms are generally used in describing *Pecten*, the two ends correspond to the anterior and posterior ends of the ventricle in most forms of lamellibranchs. The posterior aorta is much the smaller of the two, leaves the heart ventral to the intestine (actually anterior to it) and divides immediately after leaving the heart, into two vessels, one of which, the smaller, follows along the intestine, supplying it and surrounding portions with blood. The other vessel turns almost at right angles upon leaving the aorta and enters the adductor muscle, where it divides into a system of vessels that supply the muscle with blood.

The anterior aorta is much larger than the posterior aorta, and supplies all of the remainder of the body. It leaves the ventricle dorsal to (actually posterior to) the intestine and very soon gives rise to a vessel which passes into and supplies the wall that separates the pericardial cavity from the mantle chamber. From the pericardium the anterior aorta follows along the postero-dorsal border of the liver to the base of the ear. Here it gives rise to the branch (Fig. 3, *ppa*) which passes posteriorly to the extreme upper margin of the mantle that lines the ear, giving off along its course a number of branches, which supply this portion of the mantle. Here it divides into two vessels, a right and a left, each of which bends abruptly ventrally (Fig. 5, *ppa*) and follows along the margin of the respective mantle lobe about opposite the line of attachment of the infolded ridge of the mantle, alongside but external to the pallial nerve.

Very fine branches are given off from these vessels all along their courses, which further divide to form systems of capillary spaces that are finest and most numerous near the margins. Some of these capillary spaces are large enough to be injected with starch mass, and I have a preparation of the mantle lobe from which only the infolded ridge has been removed, that was dehydrated, cleared and mounted in balsam, in which the whole system of vessels can be traced. A gelatin mass not only fills the spaces mentioned, but passes out between the cells so that in sections it may be seen to be diffused throughout the tissue. This seems to hold good for all other parts of the body with the exception of the gills, in which organs the mass is more completely, but not entirely, confined to the blood spaces. The indication therefore is, that the blood spaces are not confined vessels, and that the blood functions as both blood and lymph. The posterior pallial vessel may be traced far anteriorly, gradually diminishing in size along its course. Here it finally joins the anterior pallial vessel. The anterior pallial artery (Fig. 3, *apa*) leaves the anterior aorta very near the cartilage and runs directly to the anterior border of the hinge region of the mantle, giving off vessels to this portion of the mantle on the way. Here it branches into right and left vessels, each of which bends abruptly ventrally (Fig. 5, *apa*) and pursues a course along the anterior border of the mantle similar to that taken by the posterior pallial artery at the other extremity of the animal.

Along the anterior border of the mantle, near the dorsal line, the vessel is rather small and slightly broken in its course. It may be possible that this represents the border line between the posterior and the anterior pallial arteries. There are other reasons for believing that a large share of the animal is morphologically equivalent to the posterior portions of other forms, and that the anterior portion is greatly reduced. This has received attention in another place.

Several vessels leave the anterior aorta to supply the liver and stomach. Most prominent among these is a vessel which leaves the aorta between the points of origin of the anterior and posterior pallial arteries. This bends out toward the left side of the liver, where, in injected specimens, it is very conspicuous, passes ven-

trally and sends branches to the major part of the liver and to the stomach.

A short distance in front of the cartilage the anterior aorta bends ventrally, passes through the liver and gives off a few small branches to it, sends a vessel to the palps in passing, and passes on to supply the foot and the visceral mass. The vessel that supplies the foot (Fig. 3, *fa*) leaves the aorta a short distance ventral to the mouth, passes along the body wall until the foot is reached, and extends into the foot along its dorsal border. Just before entering the foot this, the pedal artery, gives rise to a small vessel that passes posteriorly along the single retractor muscle of the foot, supplying it with blood. From the point of origin of the pedal artery the aorta extends into the visceral mass, following along the enlarged portion of the intestine that leads away from the stomach, and supplying this and other portions of the intestine and the reproductive organs with small and with large branches. The enlarged portion of the intestine that comes from the stomach is especially well supplied (compare Figs. 2 and 3), there being numerous small branches that are given off directly from the aorta, and large branches that follow along on the different sides of this portion of the intestine and likewise supply it with branches. A short distance ventral to the foot a large branch leaves the aorta and passes postero-ventrally to divide again and form small branches that supply the remaining loops of the intestine and the postero-ventral portions of the reproductive organs.

This completes what might be called the systemic arterial system. Beginning with the heart the system ends in the capillary spaces of the various organs. This system is most easily injected through the vessel in the suspensory membrane of the gills that is farthest from the adductor muscle (Fig. 1, *bv*), with a hypodermic syringe, injecting toward the heart. If a starch mass that will not pass through the capillary spaces is used, all of the vessels thus far described will be injected, as will also the veins that return blood from the gills, as this vessel is the one that returns blood from the gills to the heart. If a gelatin mass is used all of the systems may be injected, but as the injecting mass may pass out of the spaces, between the cells of the various organs, such injection does not aid in tracing the course of blood flow.

The systemic veins (Fig. 4) that collect the blood that is supplied by the systemic arteries, from the various organs of the body, may be injected from several different vessels. They may be injected by pushing the needle beneath the membrane that covers the posterior surface of the adductor muscle. A large blood space occupies this position, into which the needle is inserted and the mass injected fills the systemic veins. Another point from which these veins may be injected is from one of the superficial vessels of the visceral mass. These vessels are very conspicuous, and may be very easily picked up with the needle. Still another vessel is the vein that returns blood from the liver, which may be seen on the left side of the animal anterior to, but near the large artery that supplies the liver. Injecting any one of these vessels will to a greater or less extent inject the others, but there does not seem to be an entirely free communication between them. They all carry blood to the kidneys, and seem to empty into a common sinus on either side, that lies alongside the kidneys in the walls of the visceral mass. The sinuses of the two sides are connected beneath the adductor muscle, but it frequently happens that a complete injection of the system is not obtained from an injection from any one of the veins mentioned. Just where the obstruction lies in such cases has not been determined. It has been noticed that obstructions are more likely to be encountered in injecting from the veins of the visceral mass than in injecting from any of the others.

Inasmuch as blood spaces are cut in removing the muscle from the shell, it has been found desirable in injecting this system of vessels to wedge the valves open and to inject from the posterior surface of the adductor muscle. In injecting after the animal is removed, a considerable quantity of the injecting mass is sure to escape at the ends of the muscle.

The position of the veins may be seen in Fig. 4. A large vein comes from the liver, another from the foot, and the veins in the muscle unite to form a more or less definite sinus along the dorsal border of the muscle, and two smaller ones on the antero-ventral side of the muscle. These sinuses unite near the anterior ends of the kidneys. A series of vessels from the visceral mass unite along the borders of the kidneys and finally connect with these

sinuses. Most of the blood from all of these organs is distributed to the kidneys through systems of capillary spaces. The branching of these vessels is not conspicuous on the surface of the kidneys, but is better seen by cutting the kidneys open. That not all of the blood necessarily traverses the capillary spaces of the kidneys is indicated by the fact that injections of the systemic veins frequently fill the veins that carry the blood away from the kidneys as well as those leading to it. This is much more frequently the case when injecting from the posterior surface of the adductor muscle than when injecting from other places, and seems to be dependent upon a direct connection between the vessel in question and the sinuses on the antero-ventral surface of the adductor muscle near the dorsal ends of the kidneys.

Of the blood that leaves the heart, only that which goes to the mantle remains to be accounted for. This is collected and returned directly to the heart (Fig. 5, *pv.*)

All of the blood that leaves the kidneys is conducted to the gills. The blood from each kidney is collected into a sinus that runs along the border of the kidney that is applied to the adductor muscle. This sinus, which also seems to receive blood from the sinuses on the anterior and ventral surfaces of the adductor muscle, bends abruptly ventrally over the anterior end of the kidney and is continued on the lower border of the suspensory membrane of the gill (Fig. 1, *ba*) to the posterior end of the gill, supplying the gill with branches throughout its length.

Blood vessels leave the vessel that carries blood from the kidney, opposite each of the inter-lamellar junctions of each of the gills supported by the suspensory membrane. Each of these branches is continued along the free border of the membrane that forms the inter-lamellar junction (Fig. 7, *ba'*) until it reaches the free edge of the lamella, the edge that is not attached to the suspensory membrane. That is, if the branch supplies an outer gill, it leaves the suspensory membrane along the free border of an inter-lamellar junction and crosses over to the free border of the outer lamella of this gill. Here the vessel is continued down the enlarged, modified filament that is concerned in the formation of the inter-lamellar junction (Fig. 7, *ba''*) giving outside branches through each of the inter-filamentar junctions

(as long as these are composed of tissue that can carry blood vessels)¹ and so supplies the various filaments of the lamella. The blood thus distributed finds its way around the margin of the gill through small blood spaces and is continued up the other lamella of the gill, the blood of the small filaments being gradually collected through the vessels of the inter-filamentar junctions into the vessels of the large filaments (Fig. 7, *bv'*), and by these poured into a vessel that lies just beneath the vessel that supplies the gill and runs parallel with it (Fig. 1, *bv*). This vessel receives all of the blood from both of the gills of the side, and carries it directly to the corresponding auricle of the heart. Just before the vessel empties into the heart it receives a rather large vessel from the corresponding lobe of the mantle, which returns the blood that was sent to the mantle back of the heart.

To sum up the course of the circulation of the blood briefly, it will be seen that of the blood that leaves the heart only that which is sent to the mantle is returned to the heart after traversing a single set of capillary spaces; that a small portion of the blood sent to the adductor muscle (that which is collected by the sinuses on the antero-ventral portion of the muscle) may be returned after traversing two sets of capillaries — those of the adductor muscle and those of the gills; and that the greater portion is returned only after traversing three sets of capillaries — those of the general system, those of the kidneys, and those of the gills.

The reasons for this arrangement of the circulatory system are at least in part not hard to find. The blood which passes to the mantle loses some of its nourishing materials, but as the mantle lobes are thin and are bathed over such a large portion of their surfaces by a current of water, in which there is an abundance of dissolved oxygen, respiration, no doubt, takes place direct, and the blood has no need to pass through the gills to get a supply. Again the work of the mantle is not of such an active nature as to load the blood with nitrogenous wastes. It seems likely that the amount of nitrogenous waste in the blood that has traversed the mantle is so small that it

¹ The inter-filamentar junctions near the free margins of the gills are composed of cilia only.

would diminish the proportion of nitrogenous waste in the blood, if this blood were added to the blood that passes through the kidneys.

The blood that goes to the general system must in its progress lose a considerable portion of its oxygen, and in all portions except around the alimentary canal (where there is, of course, a decided gain) also food materials, and gain from the tissues a considerable amount of nitrogenous and carbonaceous wastes. It is then essential that such blood should go to the excretory and respiratory organs to get rid of these waste products and to gain oxygen. Inasmuch as the heart provides for but a single circulation it is necessary that the capillaries of these organs be traversed before the blood is returned to the heart. Why it is arranged so part of the blood may dodge the kidneys and be carried directly to the gills is not nearly so evident. Possibly the periodically great activity of the adductor muscle causes the blood to move through it so rapidly that the small kidneys cannot take care of it and properly perform their function, and the other channel is provided to carry the surplus away to the comparatively extensive gills where the increased flow can be taken care of with greater ease. It is, of course, essential that the amount of oxygen in the blood at such times shall not be reduced. It is at any rate evident that there is a possibility that part of the blood that is returned from the muscle, liver, etc., may not pass through the kidneys, for when starch injecting mass is injected through a vessel that carries blood from one of the kidneys to the gills, not only are the kidney and the gills injected, but part of the mass usually finds its way into the adductor muscle, liver, and other organs of the body.

The rate of the heart beat is slow, and as in other lamellibranchs is, no doubt, dependent upon the temperature of the animal as well as on other factors. The auricles and ventricle become very greatly distended during diastole, and contract so that their cavities are almost entirely obliterated in systole.

NERVOUS SYSTEM.

The three pairs of ganglia that are usually found in lamellibranchs are present in this form, but they differ greatly in size and they are not all placed in the usual positions.

The cerebral ganglia (Fig. 6, *c_g*) are placed some distance ventral to the mouth, just beneath the outer covering of the body. They, like the other ganglia, are yellowish in color, and may frequently be faintly seen through the covering of the body. Each cerebral ganglion is somewhat elliptical in outline with the long axis directed dorso-ventrally and has a rather distinct swelling on the ventral (actually anterior) and outer side (the side away from the median plane of the body) (Fig. 9, *c_g*). The anterior end of each cerebral ganglion presents a forked appearance, due to the origin of two large nerve cords. The inner and ventral one of these two cords (Figs. 8 and 9, *cc*) is the commissure that joins the two cerebral ganglia. As the ganglia lie some distance ventral to the oesophagus, this commissure forms a long loop that passes dorsally around the oesophagus just posterior to the mouth. The outer and posterior of the two large cords that leave the anterior end of each ganglion is the anterior pallial nerve (Figs. 6, 8 and 9, *apn*). This runs parallel with the commissure as far as the oesophagus and is then continued along the side of the liver, and in the mantle, to the margin of the mantle in the region of the anterior ear of the shell, where it joins by several branches the circumpallial nerve (*c_pn*) that follows along the margin of the mantle near the bases of the tentacles and eyes. The circumpallial nerve will receive attention later.

Between the points of origin of the cerebral commissure and the pallial nerve, a small nerve (Figs. 8 and 9, *pn*) leaves the ganglion to be continued dorsally, and to supply the labial palp.

From the inner, ventral surface of each cerebral ganglion, a little in front of the middle, the cerebro-pedal connective leaves to join the pedal ganglion of the same side. The cerebro-pedal connective is smaller near the cerebral than the pedal ganglion (Fig. 9, *cpc*) and bears a ganglionic swelling on its outer side very near the pedal ganglion.

In the acute angle formed by the surface of the cerebral ganglion with the cerebro-pedal connective, a small nerve (*otn*), the otocystic nerve, leaves the ganglion to be continued around the dorsal surface of the cerebro-pedal connective to the otocyst of the same side.

Posteriorly the cerebral ganglia taper rather gradually into the cerebro-visceral connectives, which run along the sides of the visceral mass very near the adductor muscle, until the visceral ganglia are reached.

The pedal ganglia lie very near each other (Fig. 9, *pg*), so the commissure that connects them is short and broad and presents ordinary ganglionic structure. They are separated from the cerebral ganglia only by a short interval, and lie anterior and slightly ventral to them, some distance dorsal to the base of the foot. They lie so near the surface that their color may frequently be distinguished through the body wall beneath the mouth. Two large nerves (*fn*) leave each pedal ganglion to be continued into the foot, where they supply the muscles of the foot and probably the byssal gland. The swellings on the cerebro-pedal connectives near the pedal ganglia have already been described. The otocystic nerves, which usually leave the cerebro-pedal connectives near the pedal ganglia, in this form originate directly from the cerebral ganglia near the point where the connectives leave the ganglia.

The visceral ganglia (Figs. 6, 8 and 10, *vig*) are by far the largest and most complicated of the ganglia, and from them nerves are sent to most parts of the body. They are situated on the antero-ventral surface of the adductor muscle, nearly opposite the external openings of the kidneys. They are imbedded in a mass of connective tissue and are fused to each other, so the commissure that connects them is nearly as broad as the ganglia themselves and shows ganglionic structure. The chief indication of the presence of a pair of ganglia is the arrangement of the nerves that leave them, and of the cerebro-visceral connectives that join them. The ganglia are divided into very definite regions, each of which is connected with definite bundles of nerve fibers and, no doubt, has a particular function to perform. I have not had time to make a detailed study of the structure and nerve tracts of the ganglia, but I am satisfied that there is much more complexity than is ordinarily attributed to the ganglia of lamellibranchs. The dorsal surfaces of the ganglia are quite smooth, but when seen from the ventral surface (Fig. 10) the regions that are indicated in the figure are always visible. On each cerebro-visceral

connective, just before it joins the ganglion proper, there is a ganglionic swelling (*x*) that supplies one of two roots of a nerve (Figs. 6, 8, and 10, *bn*) that leaves in an antero-dorsal direction along the border of the excretory organ, to bend ventrally and posteriorly in the suspensory membrane of the gills, and supply the gills of the corresponding side. Between the points where the cerebro-visceral connectives join the visceral ganglia on the ventral side, there are four rather distinct swellings, with three less distinct swellings posterior to them. Extending laterally from the outer side of each ganglion is a somewhat flattened ridge (Fig. 10, *y*) from which all of the pallial nerves from this ganglion originate. These nerves (Figs. 6 and 8, *ppn*) pass laterally, posteriorly and anteriorly along the surface of the adductor muscle, to meet the mantle lobes and to be continued to the margins, where they unite with the circumpallial nerves. It will be noticed that they unite with the circumpallial nerve at intervals throughout the greater length of this nerve. As the pallial nerves that leave the visceral ganglia in most forms pass directly to the posterior portion of the mantle, the distribution in this form may be looked upon as evidence that all of this portion of the mantle belongs morphologically to the posterior portion of the animal.

Other nerves leave the dorsal surface of the visceral ganglia near their posterior ends, and enter the adductor muscle directly. The nerves that supply the posterior division of the muscle are continued along the ventral surface of the anterior portion of the adductor muscle until this posterior portion is reached. Small nerves also leave the ventral side of the ganglia and penetrate the visceral mass.

All of the ganglia are well supplied with nerve cells, there being very many large polar cells present, but the number of the cells is far greater and their arrangement more complicated in the visceral than in any of the other ganglia.

Nerve cells are also to be found in the circumpallial nerves and in the branchial nerves. So abundant are the nerve cells in the circumpallial nerves that they assume the structure of ganglia. The nerves by which they are connected with the visceral and cerebral ganglia contain no ganglionic cells. From

the structural standpoint we would accordingly be justified in considering the circumpallial nerves as separate ganglia, and the nerves connecting them with the visceral and cerebral ganglia as connectives.

The circumpallial nerves of the two lobes of the mantle are connected with each other anteriorly and posteriorly near the hinge line (Fig. 8, *cpn*). They are not of constant diameter, but suddenly increase or diminish in size so that they have a rather irregular appearance. They lie just inside, that is, toward the median plane of the body, of the large pallial arteries that supply the mantle margin, about opposite the line of attachment of the infolded ridge. From them nerves are sent to the eyes and tentacles, to the infolded ridge and to the pallial muscles. Very likely the pallial muscles are partially supplied from the pallial nerves that come from the visceral ganglia, but of this I am not sure.

It seems probable that the ganglionic structure of these nerves has been developed to meet the needs of the very complex margins of the mantle. The development of ganglia in the immediate region of the sense organs is an indication of the ease with which such centers may be established when need arises.

The branchial nerves are supplied with ganglionic cells throughout their length. These are present not only along the borders of the gills, but from the points where the nerves originate to their extremities. The almost constant activity of the gills no doubt renders such an arrangement desirable. No other nerves or connectives in the body seem to be abundantly supplied with ganglion cells.

The whole nervous system is modified to meet the special needs of the animal. The cerebral and pedal ganglia are small, corresponding with the slight development of the anterior parts of the body and of the foot. The visceral ganglia are highly developed, corresponding to the excessive development of the parts that are supplied by these ganglia. Accessory centers have also been developed in the margins of the mantle and in the gills.

It seems that many students of Mollusca hold that the lamellibranch ganglia have been derived from a gastropod-like type, a

type that possesses at least one pair of ganglia, the pleural, that are not commonly found in lamellibranchs. This view seems to be based largely upon the acceptance of a hypothetical type for a primitive mollusk that seems to me to be a much better ancestor for the gastropods than for the other classes of the Mollusca.

PHYLOGENY.

The hypothetical primitive mollusk that has persistently been offered for our consideration, and has found its way into a number of text-books, among which is Lang's "Text-Book of Comparative Anatomy," has the dorsal portion of the body covered by a conical shell, the foot flattened and adapted for creeping, a head fold that may be protruded from beneath the shell, a pair of plumose gills, and a nervous system with at least four pairs of definite ganglia, cerebral, pleural, pedal and visceral. *Distinctly gastropod throughout.*

If the development of animals is to be considered of any importance in pointing their possible lines of descent, and as long as embryo chicks have gill arches our belief has good foundation, it would seem that in those mollusks whose eggs are not loaded with yolk, whose embryos are not modified for protection in brood pouches, and do not have long larval histories that call for special modifications to enable them to cope with enemies and to get food, the embryos might be suggestive.

The presence of unlimited food and protection always tend to destroy characters. Thus we find that parasitic forms may have entirely lost organs that must have been well developed before the animals took to parasitic lives. The presence of a quantity of yolk furthermore frequently must have mechanical effects on the developing embryo that cause direct modification. Again those embryos that pass through long larval histories exposed to the competition of forms that would eat their food and other forms that would eat them, must necessarily be exposed to the same evolutionary factors, whatever they may be, that adult animals are exposed to and we would accordingly expect adaptive modifications in them.

There are many lamellibranchs, and not a few gastropods, that do not seem to be seriously modified by any of these fac-

tors and when their embryos are examined every one must be struck with their close resemblances. These embryos would seem to point to a free swimming ancestral form that obtained its food by means of surface cilia.

The first living forms that made their appearance on the earth must have used non-living substances for food. What the nature of these substances were, whether they were of a comparatively simple nature, like those that are used by our green plants to-day, or whether they were of an entirely different nature, we have no means of knowing, but it is evident that their food was not alive.

Then came the discovery by some form that the protoplasm of other forms could be used for food. This must have been the first great factor that led to the competition of forms and called for the improvement of bodily machinery among living things, to aid in the struggle thus begun, the struggle to get food and to escape from being used as food. As Professor Brooks has indicated,¹ this would naturally lead to the discovery and colonization of the bottom of the ocean because of the greater advantages it offered both for capturing food and in affording means of protection. This introduces the further element into the competition, of some positions being far more favorable than others, and as the struggle for position increased, a struggle that has never ceased, the competition, especially between close relatives, must have become very severe.

These factors, with the struggle dependent upon them, must have caused changes in structure (in the improved machinery that aids forms in getting food and in keeping from being used as food) to change very rapidly and it seems very plausible that in a comparatively short time in those days when forms were of simple structure and this keen competition was begun, the foundations of the great types of animal structure were laid.

We know that among our earliest fossils are to be found both lamellibranchs and gastropods, and it is back in the earlier time that we must look for the changes that have resulted in the formation of these classes.

¹ Brooks, "The Origin of the Oldest Fossils and the Discovery of the Bottom of the Ocean," Smithsonian Report for 1894 (also Salpa).

We may possibly conceive that the ancestor of the Mollusca was among the early ones to recognize the advantages of the ocean bottom, and that its race soon developed a protective shell, if this had not started to form before it became a dweller on the bottom. The shell would offer protection, but would, because of weight, interfere with rapid movement. As enemies became able to get beneath its armor the shell became thickened and was made to cover the animal more completely, but the added weight interfered still more with rapid movement.

At this time we need not suppose that the animal had more than the very simplest nervous system, hardly more than that needed by a trocophore larva, for it would probably be dependent upon simple bands of cilia, or at the most a movable mouth portion, for getting its food. There is no reason for supposing that this animal had yet developed gills, or if gills were present they would hardly be more than simple folds of the mantle.

As competition became more severe, animals of this kind were in need of better protection, and it is possible to conceive that there might have been evolved two types, one that inclosed itself in a bivalve shell, crawled into the mud, and obtained its food by capturing the forms brought to it in a current of water of its own creation, the other, more like the *hypothetical primitive mollusk that has been described*, which retained a single shell and got its food by creeping over the bottom and picking it up directly. The first form would still have a simple head apparatus and would need new nervous centers only to provide for the mechanism necessary to crawl into the mud and the mechanisms necessary to create the current of water and capture the living forms from it. The second form would have a more complicated head apparatus and would need nervous centers to supply it and to supply the organ by means of which it was enabled to creep. In these differences in life, and in the consequent differences in structure, it seems reasonable to look for the differences in their nervous systems. If this conception is anything like true, from very early times there was no similarity in the method these two groups used in getting food. One has finally developed a remarkably satisfactory method of straining out living particles that serve it as food, from a current of water of its own formation, and

is thus able to leave little of its surface exposed to the attacks of enemies. The other has developed one of the most complicated of machines in connection with its mouth to aid it in getting food.

As the head apparatus of the one type has increased in complexity, there has been greater need of ganglia to supply it, but in the whole line of development of the other type there has been no complicated head apparatus. About all of the actual evidence that we have of the presence of pleural ganglia in lamellibranchs is that given by Pelseneer,¹ who finds in *Nucula* and some other forms, that each anterior ganglionic mass is so shaped that it is possible to consider it as two ganglionic masses, and further that the connective that runs from this mass to the pedal ganglion is connected with this mass by two roots. The interpretation that he has put on this is that the two apparent divisions of the ganglion represent respectively the cerebral and pleural ganglion, and that the roots of the connective represent the cerebro-pedal and pleuro-pedal connectives that have become fused before reaching the pedal ganglion. My own view, discussed in another paper² is that the apparent division into two ganglionic masses is superficial, and due to the swellings accompanying the origins of nerves, and that one of the cerebral ends of the connective may be the central end of the otocystic nerve which is fused for the greater part of its length with the connective, but, unlike most forms, is free near the ganglion. This view seemed to me most reasonable as Stempell³ has found that in *Soleyma togata*, a supposed near relative of *Nucula*, the otocystic nerve arises directly from the cerebral ganglion and is separate from the connective throughout its length. So far as I know, the instance given by Stempell is the only one that has heretofore been reported where the otocystic nerves originate from the cerebral ganglia, and are free from the cerebro-pedal connectives throughout their length. *Pecten tenuicostatus* has the same arrangement. In this form the position of the ganglia, connectives and otocysts is such that it is a very simple matter for the

¹ Pelseneer, "Contribution à l'étude des Lamellibranchs," *Arch. de Biol.*, XI., 1891.

² Drew, "The Life-History of *Nucula delphinodonta*," *Quart. Jour. of Micro. Sci.*, Vol. 44, Part 3, New Series, 1901.

³ Stempell, "Zur Anatomie von *Soleyma togata*," *Zool. Jahrb.*, Bd. XIII., 1899.

otocystic nerves to make direct connection with the cerebral ganglia, but they do not join the ganglia at their nearest points. Instead they are continued around the connectives to join the ganglia in contact with, and posterior to them.

To me it seems probable that the separation into the two groups that have developed into the classes Lamellibranchiata and Gastropoda took place at an early date in the history of the Mollusca, probably before a complicated head apparatus was developed, and while the nervous system was of a very simple nature. If this was the case, we have no reason to search for pleural ganglia in lamellibranchs, for it is very probable that they never had them. In fact were ganglia ever present in this region in lamellibranchs, it would be more reasonable to view them as new formations for special purposes than as direct descendants from, and accordingly homologous with, the pleural ganglia of gastropods. The gastropod and lamellibranch are so different in structure and habits that we may reasonably expect important differences in their nervous systems. Gastropods and cephalopods possess accessory ganglia that have evidently been developed to perform special functions. That such centers may be comparatively easily developed is indicated by the fact that the circum-pallial nerves of the scallop are essentially such centers. Is it not then more likely that pleural ganglia have been developed in the groups that need them than that lamellibranchs, which, so far as we know, have never been more complicated than they are to-day, should have formerly possessed these ganglia and have since quite uniformly lost them?

ANATOMICAL DRAWINGS.

It sometimes happens that in making a series of drawings intended to illustrate different organs of the same animal, considerable labor can be saved by using a combination of photograph and ink. The figures of the present paper illustrate this saving much better than is usually the case. To draw the margin of the mantle, with its large number of sense organs, requires both time and patience, and were it necessary to draw it for each of the figures where it necessarily occurs, one would be tempted to abandon it altogether.

It occurred to me, while engaged in drawing this margin, that possibly it could be photographed on a paper of a quality that would allow pen drawing and thus save redrawing it. After some trials a platinum paper was found that met the requirements but I was surprised to find how much blacker Higgins ink was than the blackest print I could make.

Evidently, however, any mark that would take at all in making a zinc etching would print the same color as the rest when being put through the press, so one of the poorest of these photographs was finished with Higgins ink and sent away to have a zinc etching made from it. The result was perfectly satisfactory. It will be seen that the margins on Figs. 1, 2, 3, 4, 6, 11, and 12 are all alike. The margin of Fig. 1 is the only one that was made with pen and ink. Fig. 11 is a print of a negative made from this margin before the rest of the animal was drawn. Taking a print similar to that shown in Fig. 11, with pen and ink there was drawn into it the organs shown in Fig. 12. Fig. 2, before the alimentary canal was added, was the figure from which the photograph resulting in Fig. 12 was taken. The margin of Fig. 12 is then a photograph of a photograph of an ink drawing. The original of Fig. 12 was then worked on to form Fig. 2 just as the original of Fig. 11 was worked into Fig. 1. Figs. 3, 4 and 6 are all worked onto prints similar to that shown in Fig. 12. In the original paper in which these figures were published a number of others were based on photographs in a similar way. The saving of time in the paper probably amounted to more than one half, and certainly may be of importance to others. I have no doubt that photographs may also be made the basis of brush work, but great care will be necessary in such cases in getting the proper printing value. While the figures accompanying this paper show no evidence that the photograph and the ink had different printing valves, they would have been very unsatisfactory had they been reproduced by some other processes.

SUMMARY.

Circulatory System. — The large size of the animal makes it possible to inject the vascular system successfully. Blood from the mantle is returned immediately to the heart. Most of the

blood from other portions is carried to the kidneys, from which it is carried to the gills, and then back to the heart. A portion may dodge the kidneys and go to the gills. Blood seems to act both as blood and lymph. (See pp. 227-234 and Figs. 3, 4, 5 and 7.)

Nervous System.—The cerebral and pedal ganglia are small and somewhat removed from their usual positions. The visceral ganglia are very large and complicated in structure. The circum-pallial nerves and the branchial nerves have ganglion cells throughout their length. The otocystic nerves originate directly from the cerebral ganglia. (See pp. 234-239 and Figs. 6, 8, 9 and 10.)

Phylogeny.—Ontogeny and the probable conditions that have resulted in the complication of structure, both seem to indicate that the division of the Mollusca into lamellibranchs and gastropods, took place at an early time, before the ancestors had attained much complexity of structure.

There seems to be no reason for believing that lamellibranchs ever had more complicated head machinery than they have at the present time. If this is true they probably have never had need of more anterior ganglia than they now generally have. (See pp. 239-243.)

Anatomical Drawings.—A combination of photographs and drawings may sometimes save much time and tedious work. (See pp. 243 and 244.)

UNIVERSITY OF MAINE,
ORONO, MAINE,
November 15, 1906.

PLATE XVII.

FIG. 1. Animal as seen from the left side with the left shell valve and mantle lobe removed and with a portion of the pericardial wall cut away. A few of the blood vessels are shown. Two thirds natural size.

FIG. 2. Animal as seen from the left side with the left shell valve and mantle lobe removed, with the alimentary canal shown. Two thirds natural size.

a, auricle; *ba*, branchial artery; *bv*, branchial vein; *c*, cartilage; *e*, excretory organ; *f*, foot; *fe*, free edge of the unattached lamella of the gill; *g*, gill; *i*, intestine; *lp*, labial palp; *m*, mantle; *pa*, posterior adductor muscle; *s*, stomach; *v*, ventricle; *vm*, visceral mass.

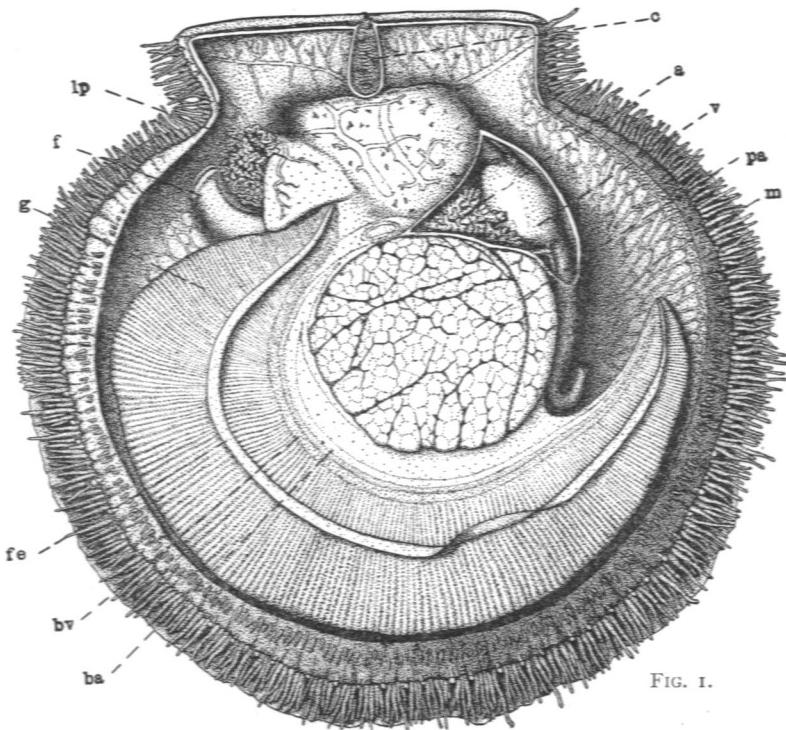


FIG. 1.

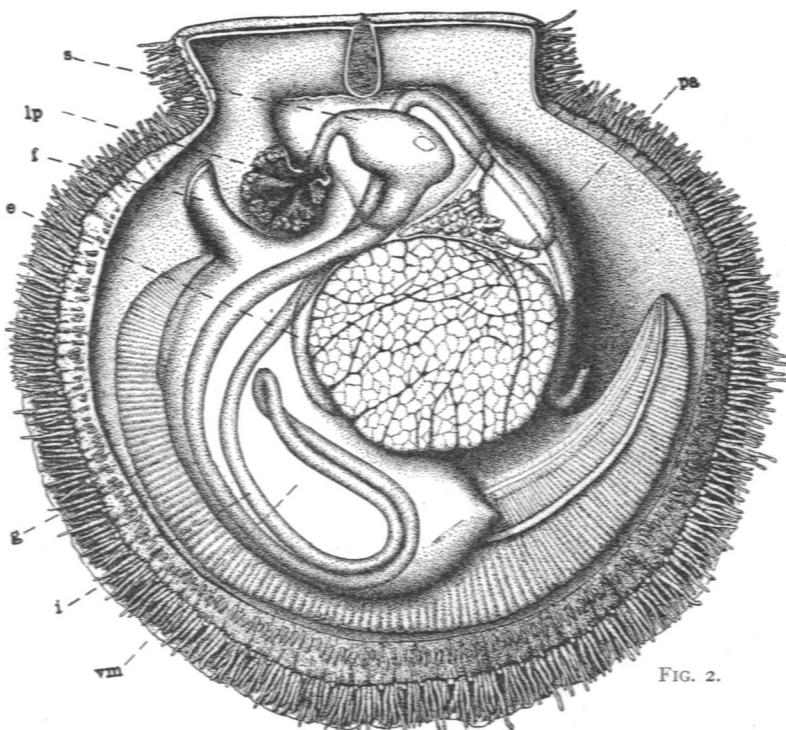


FIG. 2.

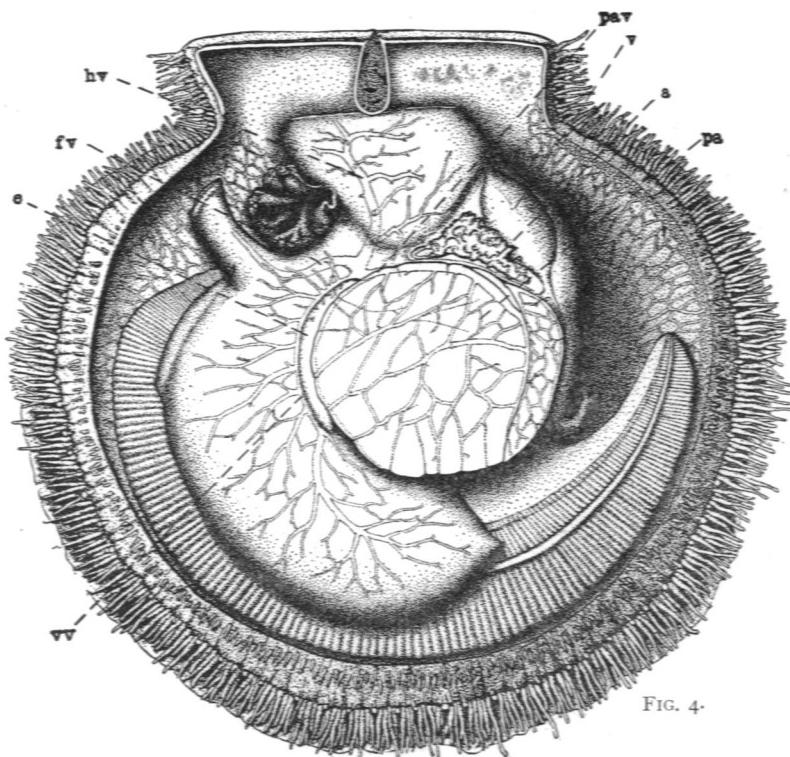
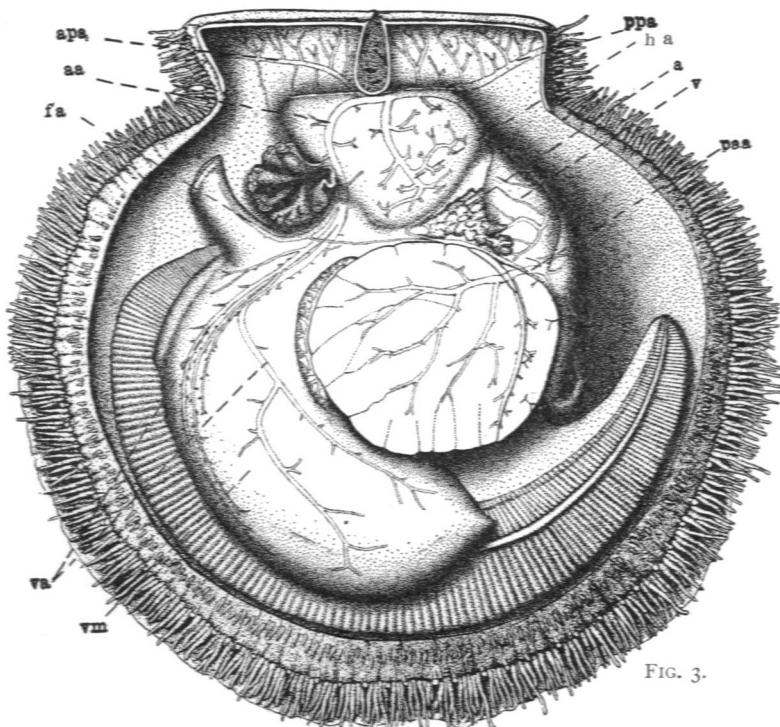
Drew del.

PLATE XVIII.

FIG. 3. Animal as seen from the left side with the left shell valve and mantle lobe removed. Drawn to show the arterial system of blood vessels. Two thirds natural size.

FIG. 4. Animal as seen from the left side with the left shell valve and mantle lobe removed. Drawn to show the systemic veins. Two thirds natural size.

a, auricle; *aa*, anterior aorta; *apa*, anterior pallial artery; *e*, excretory organ; *fa*, foot artery; *fv*, foot vein; *ha*, hepatic artery; *hv*, hepatic vein; *pa*, posterior adductor muscle; *paa*, posterior adductor artery; *pav*, posterior adductor vein; *ppa*, posterior pallial artery; *v*, ventricle; *va*, visceral arteries; *vm*, visceral mass.



Drew del.

PLATE XIX.

FIG. 5. Outer surface of the left lobe of the mantle showing the arrangement of blood vessels. Two thirds natural size.

FIG. 6. Animal as seen from the left side with the left shell valve and mantle lobe removed. Drawn to show the nervous system. Two thirds natural size.

appa, anterior pallial artery; *apn*, anterior pallial nerve; *bn*, branchial nerve; *cc*, cerebral commissure; *cg*, cerebral ganglion; *cpn*, circumpallial nerve; *cvc*, cerebro-visceral connective; *ot*, otocyst; *pa*, posterior adductor muscle (anterior portion); *pa'*, posterior adductor muscle (posterior portion); *pg*, pedal ganglion; *ppa*, posterior pallial artery; *ppn*, posterior pallial nerve; *pv*, pallial vein; *vg*, visceral ganglion.

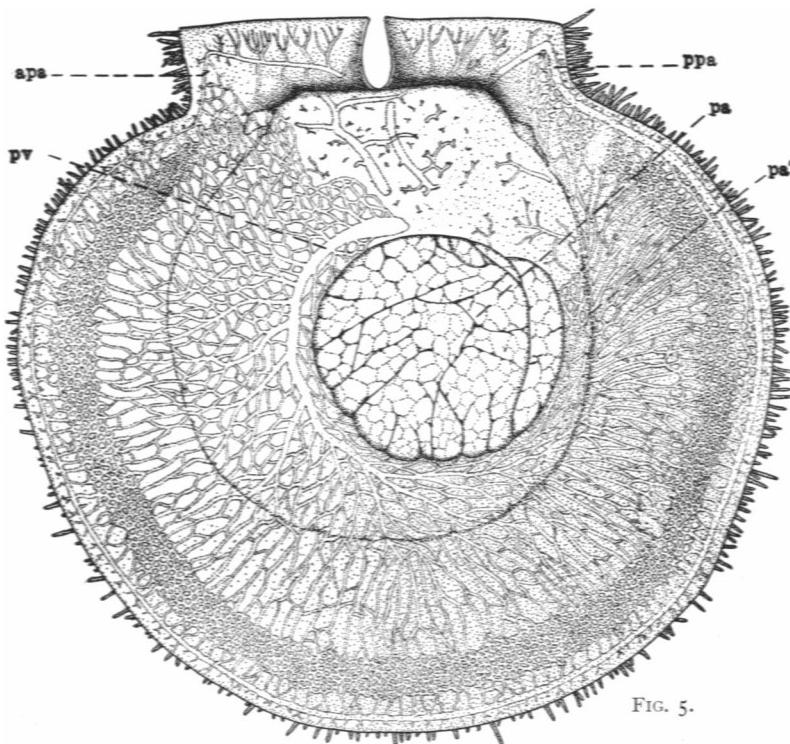


FIG. 5.

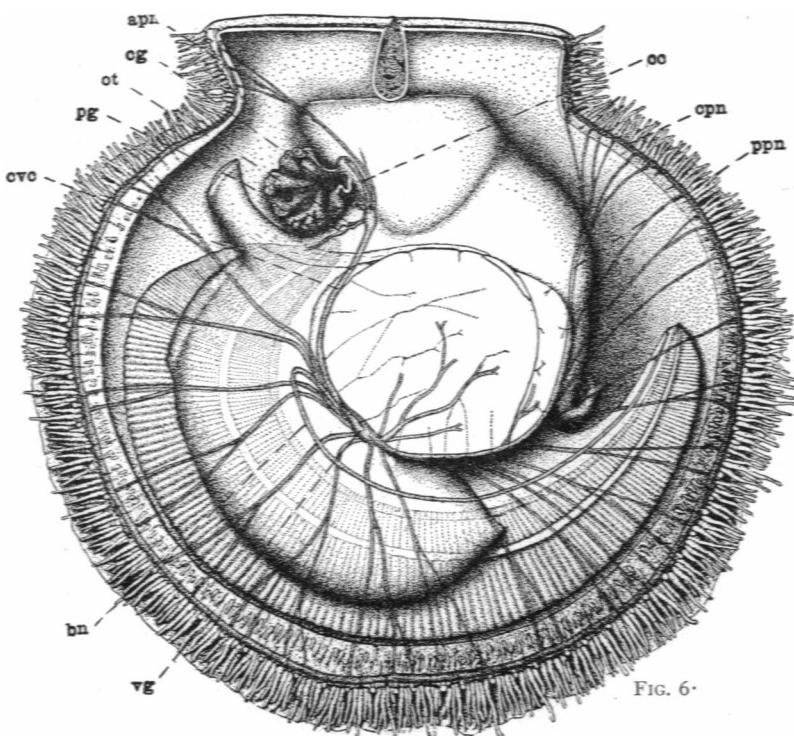


FIG. 6.

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PLATE XX.

FIG. 7. A portion of a gill showing the arrangement of parts. The figure indicates the inter-lamellar junctions cut at different levels. The further lamella is the one that was attached to the suspensory membrane and the vessel (ba') was directly connected with the vessel that supplied the gill with blood (ba , Fig. 1). This vessel follows along the edge of the inter-lamellar junction to the free edge of the unattached lamella (the one on the side nearest the observer in the figure), where it bends back and passes down the modified filament as the vessel ba'' . Branches are given off from this vessel through the inter-filamentar junctions to supply the filaments. The vessel bv' is the vessel into which the blood that has traversed the gill is collected. It in turn communicates with the vein of the gill (bv , Fig. 1). Magnified about seventy diameters.

ba' , branch of the branchial artery; ba'' , branch of the branchial artery in the modified filament; bv' , branch of the branchial vein; cr , chitinous rod; gf , gill filament; ifj , inter-filamentar junction; ilj , inter-lamellar junction; io , inhaled ostium.

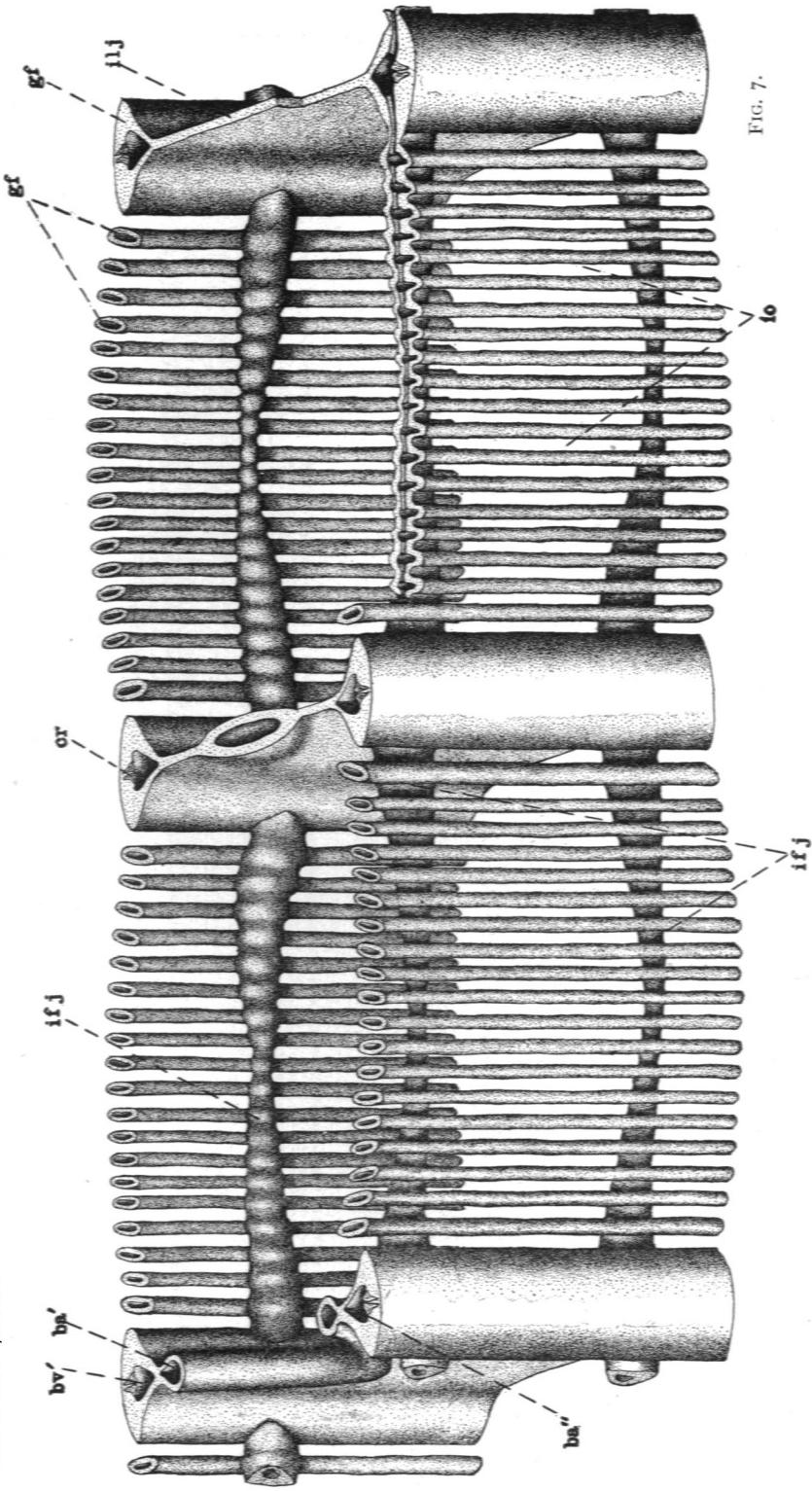


FIG. 7.

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PLATE XXI.

Fig. 23. Nervous system as seen from in front and a little to one side. Natural size. (Diagrammatic.)

apn, anterior pallial nerve; *bn*, branchial nerve; *cr*, cerebral commissure; *cg*, cerebral ganglion; *cpc*, cerebro-pedal connective; *cpn*, circum pallial nerve; *cvc*, cerebro-visceral connective; *ot*, otocyst; *pg*, pedal ganglion; *pn*, palp nerve; *pvn*, posterior pallial nerve; *vg*, visceral ganglion.

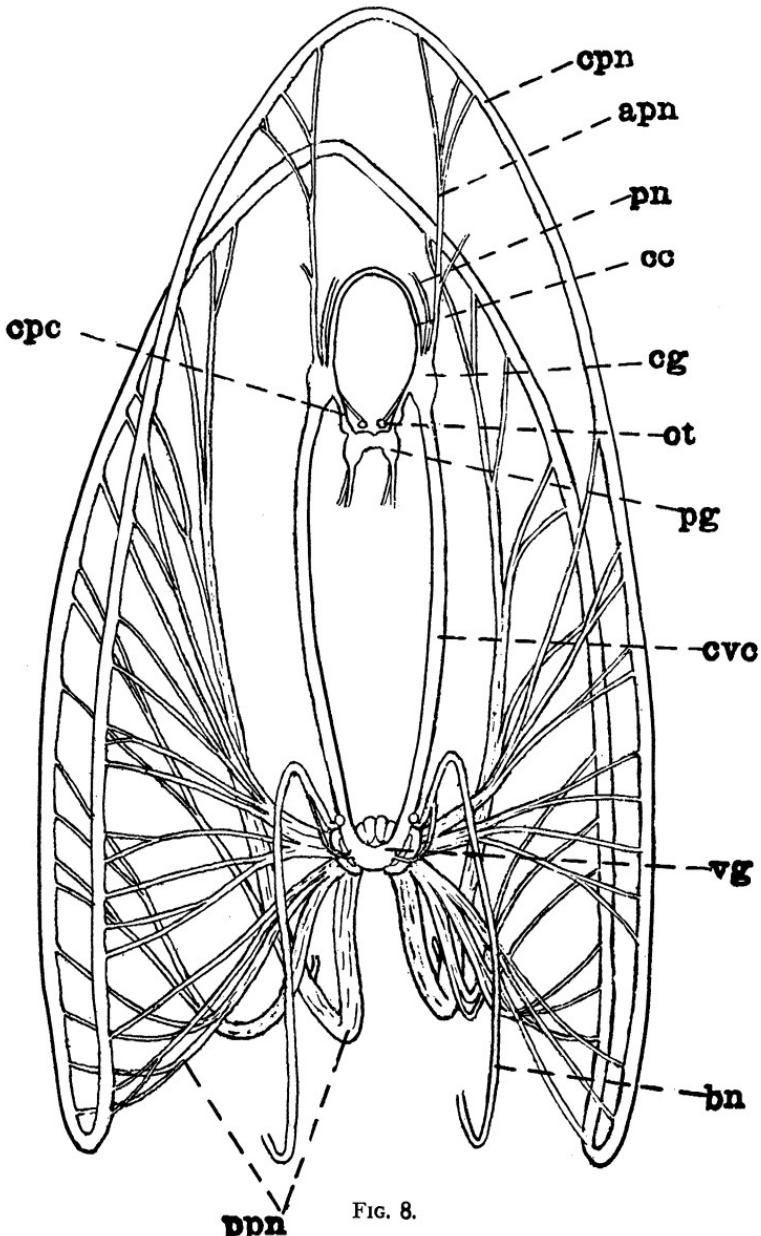


FIG. 8.

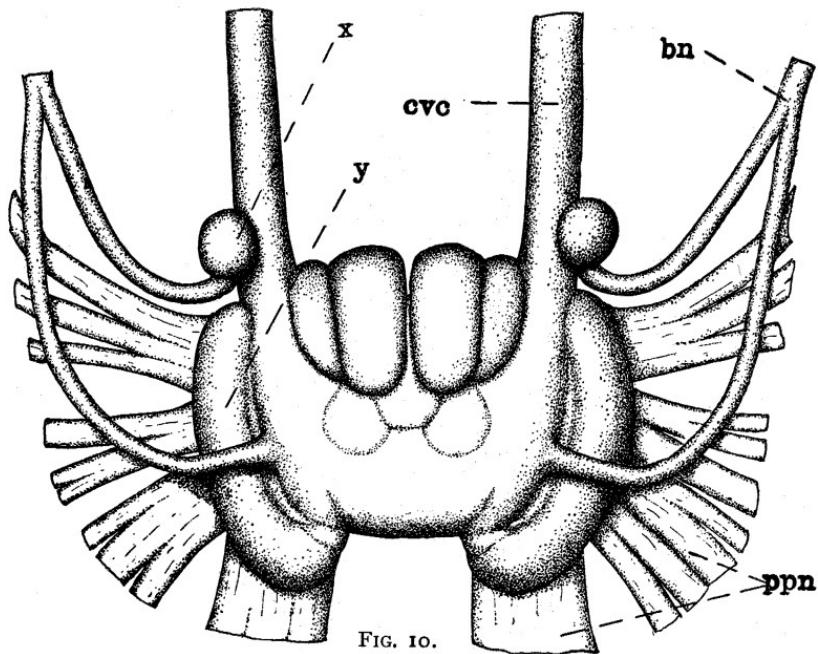
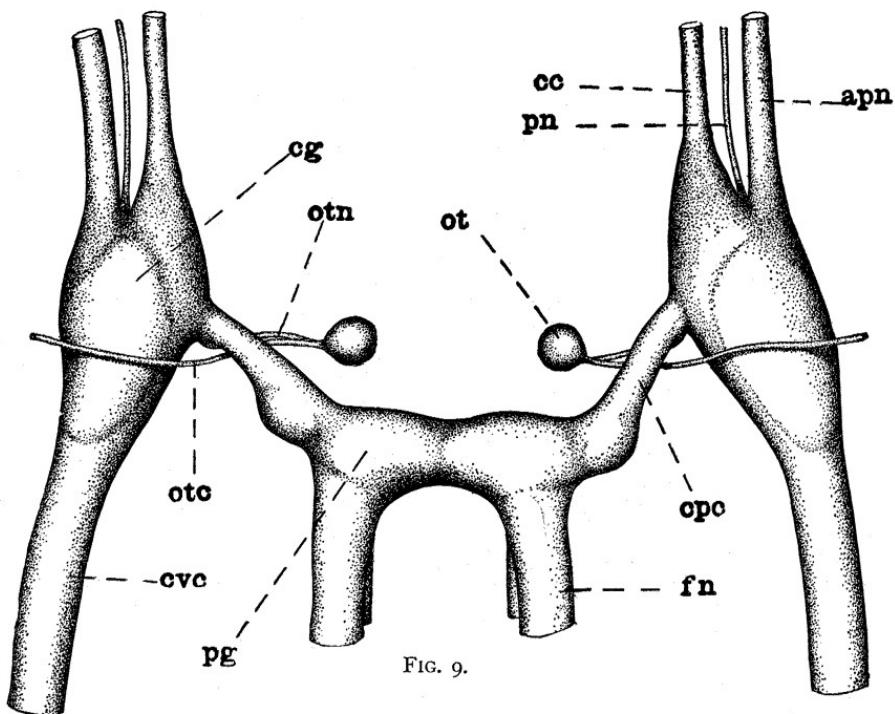
Drew del.

PLATE XXII.

Fig. 9. Cerebral and pedal ganglia with their nervous connections, as seen from the antero-ventral position. These ganglia and the otocysts lie in a mass of connective tissue and may be dissected out and mounted for study without injury. Magnified about fifteen diameters.

Fig. 10. Visceral ganglia seen from the ventral side. These may easily be exposed for study by stripping the thin muscular covering from their ventral surfaces. They are hard to separate from the adductor muscle but they may be mounted with a thin piece of the muscle and studied in position. Magnified about fifteen diameters.

apn, anterior pallial nerve; *bn*, branchial nerve; *cc*, cerebral commissure; *cg*, cerebral ganglion; *cpc*, cerebro-pedal connective; *cvc*, cerebro-visceral connective; *fn*, foot nerve; *ot*, otocyst; *otc*, otocystic canal; *otn*, otocystic nerve; *pg*, pedal ganglion; *pn*, palp nerve; *ppn*, posterior pallial nerves; *x*, swelling on the visceral ganglion from which the anterior root of the branchial nerve originates; *y*, swelling on the visceral ganglion from which the posterior pallial nerves originate.



Drew del.

PLATE XXIII.

Fig. 11. Etching made from a photograph of the margin of Fig. 1, before that figure had been completed. It will be noticed that the same margin occurs on all of the figures that show this portion of the mantle.

Fig. 12. Etching made from a photograph of a combination of a photograph and an ink drawing. The photograph was made from Fig. 2 before the alimentary canal had been worked in. Fig. 2 was drawn on a print like Fig. 11. Figs. 3, 4 and 6 are etchings of drawings made by adding various organs on prints like Fig. 12.



Fig. 11.

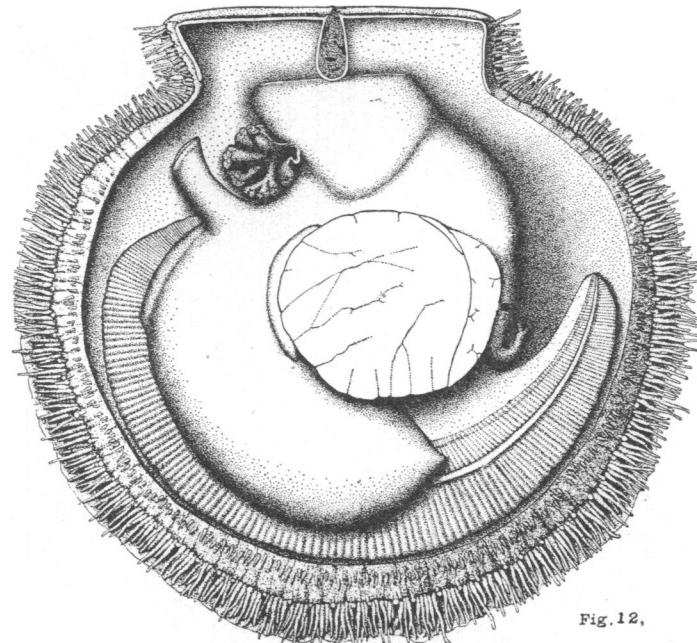


Fig. 12.